



# Effect of temperature and soil organic matter quality on greenhouse-gas production from temperate poor and rich fen soils



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## ABSTRACT

Production of carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) from peatland soil is controlled by rates of organic matter decomposition; soil organic matter (SOM) decomposition is influenced by the quality of the SOM and the soil temperature. This study determined the effect of increasing temperature and SOM quality on rates of greenhouse-gas production in lab incubations from peat soils formed under different plant functional types found in temperate rich and poor fens of southern Ontario, Canada. Peat derived from different plant functional type (sedge, shrub, and non-vascular vegetation) between the fens was composed of different amounts of SOM, lignin, and cellulose. Rates of CO<sub>2</sub> and CH<sub>4</sub> production from the lab slurries increased with increasing temperature; however, the relative increases were specific to the vegetation type overlying the soils. Anaerobic to aerobic production ratios ranged from 7% (*Chamaedaphne* soils) to >30% (*Sphagnum* soils). Ratios of potential anaerobic production (CO<sub>2</sub> to CH<sub>4</sub>) generally decreased with increasing temperature. The interaction between temperature and SOM quality was demonstrated through the range of Q<sub>10</sub> values (1.09–2.38 for CO<sub>2</sub>; 2.98–21.40 for CH<sub>4</sub>). These measures were correlated to lignin and cellulose content and the lingo-cellulose index. Results of this study indicate the variability of greenhouse-gas fluxes from peatland soils is influenced by the SOM quality derived from the overlying vegetation. As the climate warms soil temperatures will increase rates of decomposition, and this study will improve models of temperate peatland carbon cycling and can inform land management planning by providing options for minimizing carbon loss.

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## 1. Introduction

Peatlands store one-third of the global terrestrial carbon pool, despite covering just 3% of the global land surface area (Gorham, 1991). Peatlands have relatively low rates of primary production (Lafleur et al., 2005), yet organic carbon accumulation in peatlands proceeds due to concomitant low rates of decomposition (Frolking et al., 2001). Peat soil respiration is inhibited in part by elevated water table producing anoxic conditions, low air and soil temperatures, and poor quality of organic carbon substrates (Moore and Basiliko, 2006; Juszczak et al., 2013). Despite the long-term accumulation of organic carbon peatlands are the greatest global natural emitters of methane (CH<sub>4</sub>), a potent greenhouse gas with a global warming potential 25-times that of carbon dioxide (CO<sub>2</sub>) over a 100-yr period (IPCC, 2007). Thus, the CO<sub>2</sub> uptake-respiration dynamics of peatlands need to be weighed carefully with rates

of CH<sub>4</sub> emission when considering the carbon-storage function of peatlands. Rising global air temperatures will increase peatland soil temperatures, which are likely to increase rates of respiration and CH<sub>4</sub> production (Turetsky et al., 2014). Additionally, rates of CO<sub>2</sub> and CH<sub>4</sub> production are influenced by the organic substrates of the peat itself (Liefeld et al., 2012). The quality of soil organic matter (SOM) is controlled by the overlying vegetation (Heller et al., 2015); therefore, rates of CO<sub>2</sub> and CH<sub>4</sub> emission from peatlands in response to global warming will be influenced by shifting peatland species composition.

Vascular and non-vascular vegetation have different amounts of various carbon compounds depending on plant functional type (graminoid, herbaceous, woody shrub, moss) and even within a type (ex., grass versus shrub) (Lambers et al., 2008). These compounds include waxes and other lipids, pectin, simple sugars, proteins, and progressively less labile material including hemicellulose, cellulose, and lignin (Lambers et al., 2008). Because of their chemical structure and C:N:P ratios these compounds represent a spectrum of decomposability once dead plant tissue becomes incorporated in the SOM (Melillo et al., 1989; Reddy and DeLaune, 2008; Wilson et al., 2016). Moore et al. (2007) found that peatland

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leaves decayed quicker than stems, with no difference between sedge and shrub leaves. Sedge-derived peat soils lost significantly less organic carbon than heath- and tussock-derived soils in an Alaskan peatland due to higher proportions of lignin (Shaver et al., 2006). Leifeld et al. (2012) identified a strong decline in polysaccharide content with depth through the peat profile that resulted in decreased rates of respiration.

Peatland type also has a strong influence on SOM processing. The bog-poor fen-rich fen continuum is based on increasing soil pH due to increasing connection to surrounding landscapes that supply calcium carbonate, yet contain representatives from the same plant functional types (Mitsch and Gosselink, 2015). Heller et al. (2015) found increasing biochemical activity and lower proportions of lignin in SOM with increasing minerotrophic status in peatlands. Methane and CO<sub>2</sub> fluxes were greater in laboratory columns of bog peat compared to fen peat subjected to the same environmental conditions (Moore and Dalva, 1993). Analysis of a large number of sites throughout the globe revealed that the differential rates of greenhouse-gas production between bogs and fens are related to the antecedent moisture conditions and subsequent wetting event timing (Turetsky et al., 2014). Presently there is a lack of information on the comparison of rates of greenhouse-gas production from peat soils derived from equivalent plant functional types between peatland types, particularly in response to elevated temperatures.

Temperature and SOM quality been found to influence rates of CO<sub>2</sub> and CH<sub>4</sub> production in arctic (Shaver et al., 2006), subarctic (Diakova et al., 2016), boreal (Waddington and Roulet, 1996; Carter et al., 2012; Armstrong et al., 2015), temperate (Lafleur et al., 2005; Aguilos et al., 2013; Juszczak et al., 2013), subtropical (Inglett et al., 2012; Sihi et al., 2016), and tropical (Chimner, 2004) peatlands. It is well established that peatland soil respiration and methane production increase with increasing soil temperature (Conant et al., 2011; Carter et al., 2012; Wilson et al., 2016). The increased rates of greenhouse-gas production from soils due to temperature increases are described by the Q<sub>10</sub> factor – the increase in production rate for a 10 °C temperature increase—and have been found to range between 1 and ~30 (Moore and Dalva, 1993; Segers, 1998). Generally, Q<sub>10</sub> values are higher for methanogenesis than for aerobic or anaerobic CO<sub>2</sub> production (Inglett et al., 2012). This has potentially significant implications for C-cycling in peatlands in response to climate change. Significant increases in soil temperature may lead to disproportionate increases in CH<sub>4</sub> production; hence, the increased GWP of CH<sub>4</sub> combined with these increased rates of production may lead to large positive feedbacks to climate change. On the other hand, there is the potential that certain peatland vegetation can lead to poor SOM quality that can minimize rates of CH<sub>4</sub> production (Pinsonneault et al., 2016; Inglett et al., 2012). Sihi et al. (2016) suggest that with increasing temperature methanogens are able to utilize recalcitrant SOM with greater efficiency than decomposers, complicating SOM-temperature-greenhouse-gas-production generalizations.

The objectives of this study were to (1) determine the effect of temperature increases on the potential greenhouse-gas production from soils collected from a temperate poor and rich fen; (2), determine whether the overlying vegetation impacts differences in the quality of the accumulated SOM; and (3) determine whether the SOM quality differences influenced the temperature response to potential greenhouse-gas production from the peat soils. In this study soils from a rich and a poor fen in similar hydrogeologic settings were chosen, and incubation experiments were carried out on peat collected from areas of each fen dominated by sedges, shrubs, and non-vascular vegetation. Elucidation of the interaction between the SOM pool and temperature sensitivity of temperate peatland soils will inform predictions of future greenhouse-gas emissions with changing climate. It will also provide information on

the potential effect of certain target species in wetland restoration on soil greenhouse-gas fluxes.

## 2. Methodology

### 2.1. Study area

Soil samples were collected from different vegetation communities in two fens of southern Ontario, Canada. Osprey Wetland (44°15'13" N, 80°20'47" W) is a 130-ha poor fen formed in a depression of the Dundalk Till Plain. It is underlain by sandy silt till resting on top of Guelph formation dolomite (Burwasser, 1974). Peat depth at the poor fen averages 2.1 m. Mean pore-water pH is 5.3, with specific conductivity and calcium concentration 103 μS cm<sup>-1</sup> and 21 mg L<sup>-1</sup>, respectively (Radu, unpublished data). Vegetation is dominated by *Sphagnum* species *S. capillifolium*, *S. rubellum*, *S. fuscum* and *S. magellanicum*, with distinct patches of sedge (*Carex oligosperma* and *Eriophorum vaginatum*) and ericaceous shrub (*Chamaedaphne calyculata*, *Rhododendron groenlandicum*, and *Vaccinium uliginosum*) communities throughout. The Fletcher's Creek Riparian Fen (43°24'57" N, 80°7'3" W) is a 4-ha extreme rich fen formed in an area of the Guelph Formation devoid of any glacial overburden material (Duval and Waddington, 2012). The peat averages 0.8 m in depth and rests on a thin layer (<1 m) of sandy silt (Duval and Waddington, 2011). Mean pore-water pH, specific conductivity, and calcium concentration are 7.0, 890 μS cm<sup>-1</sup>, and 135 mg L<sup>-1</sup>, respectively (Duval and Waddington, 2011). The rich fen has high vascular plant diversity, dominated by many sedge species of the *Carex* genus, and shrubs such as *Cornus stolonifera*, *Rhamnus alnifolia*, *Salix candida*, and grasses such as *Calamagrostis canadensis*, *Muhlenbergia glomerata*, and *Poa palustris*. More information on the poor and rich fens can be found elsewhere (Radu, 2017 and Duval et al., 2012; respectively).

### 2.2. Sample collection

Soils were collected from three areas of each fen representing distinct vegetation types: sedges, shrubs, and non-vascular communities (*Carex oligosperma*, *Chamaedaphne calyculata*, *Sphagnum capillifolium* at the poor fen site, and *Carex livida*, *Cornus stolonifera*, and the stonewort *Chara* spp. at the rich fen site, respectively). At each vegetation community the near-surface plant residues were removed and 10-cm soil cores were collected in triplicate at 10-cm depth, on centre, using a serrated blade. Individual cores were sealed in air-tight 6 mil polyethylene bags and stored on ice for transport to the lab, where they were refrigerated until the experiment began within 48 h of collection in the field.

### 2.3. Experimental setup

To test the effect of soil temperature on production of CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O from collected peatland soil found under different vegetation types, a full factorial experiment modified from Inglett et al. (2012) was conducted. Soils were homogenized in their bags, and 10 g dry-weight of soil was placed in 60-mL clear serum bottles for analysis. Soils from each of the six vegetation communities were incubated at 5 °C in a refrigerator and at 15 and 25 °C in two Sanyo MLR-352 environmental chambers under both aerobic and anaerobic conditions. All incubations were kept in the dark throughout the experiment. The serum bottles of the soils of the aerobic treatment were left uncapped between sampling periods. Aerobic serum bottles were periodically weighed and deionized water was added on a mass-basis as required to keep soils at pre-determined field capacity moisture content. Deoxygenated water was added to the anaerobic treatment to fully saturate the soils and have ~3 mm of

**Table 1**  
Soil organic matter composition of the fen peat.

Soils under a community dominated by:	SOM (%)	Lipids, Pectin, & Sugars (%)	Protein (%)	Hemicellulose (%)	Cellulose (%)	Lignin (%)	Lignin to Cellulose Ratio
<i>Carex oligosperma</i>	91.2 ± 0.7 <sup>a</sup>	40.6 ± 4.1 <sup>a</sup>	11.4 ± 0.3 <sup>a</sup>	7.8 ± 1.6 <sup>a</sup>	19.5 ± 2.8 <sup>a</sup>	20.6 ± 1.5 <sup>a</sup>	0.43 ± 0.04 <sup>ac</sup>
<i>Chamaedaphne calyculata</i>	92.2 ± 1.1 <sup>a</sup>	34.1 ± 1.0 <sup>a</sup>	10.5 ± 0.9 <sup>a</sup>	6.7 ± 0.9 <sup>a</sup>	13.2 ± 0.3 <sup>b</sup>	35.5 ± 2.4 <sup>b</sup>	0.64 ± 0.02 <sup>b</sup>
<i>Sphagnum capillifolium</i>	92.6 ± 0.4 <sup>a</sup>	38.0 ± 2.3 <sup>a</sup>	11.7 ± 0.5 <sup>ab</sup>	8.1 ± 0.3 <sup>a</sup>	17.3 ± 0.9 <sup>a</sup>	25.0 ± 1.2 <sup>a</sup>	0.50 ± 0.01 <sup>c</sup>
<i>Carex flava</i>	90.0 ± 4.4 <sup>ab</sup>	7.7 ± 3.1 <sup>b</sup>	15.7 ± 1.9 <sup>bc</sup>	13.6 ± 1.5 <sup>b</sup>	32.5 ± 2.7 <sup>c</sup>	30.5 ± 3.5 <sup>b</sup>	0.40 ± 0.03 <sup>a</sup>
<i>Chara</i> spp.	54.1 ± 3.4 <sup>c</sup>	17.2 ± 2.4 <sup>c</sup>	11.7 ± 2.8 <sup>ab</sup>	28.1 ± 3.9 <sup>c</sup>	35.5 ± 4.5 <sup>c</sup>	7.5 ± 2.9 <sup>c</sup>	0.11 ± 0.05 <sup>d</sup>
<i>Cornus sericea</i>	82.2 ± 2.4 <sup>b</sup>	2.7 ± 0.8 <sup>b</sup>	19.6 ± 1.1 <sup>c</sup>	15.0 ± 0.7 <sup>bc</sup>	31.3 ± 1.6 <sup>c</sup>	31.5 ± 0.9 <sup>b</sup>	0.41 ± 0.01 <sup>a</sup>

Superscript letters denote significant differences ( $p < 0.05$ ) between the soil types for the corresponding soil organic matter component.

standing water in the bottles. Serum bottles for the anaerobic treatment were then capped and crimped, and remaining headspace gas was purged and replaced five times with 6.0-grade  $N_2$  gas. Each treatment was run in triplicate. Triplicate blanks were run for both aerobic and anaerobic treatments at all three incubation temperatures. Aerobic blanks contained ~20 mL deoxygenated water and were uncapped; anaerobic blanks contained the same water, and were capped and purged of  $O_2$  in the headspace as above.

Each replicate was sampled every three days over a 30-day incubation period. Following initial gas collection on sampling days the aerobic replicates were capped and crimped to trap gas produced over a 3-h incubation period. Headspace gas was collected from all replicates with an 18-gauge syringe needle and stored in 15-mL evacuated Exetainers (Labco Ltd., UK). Following collection of the anaerobic replicates the extracted headspace was replaced with 6.0-grade  $N_2$  gas. Crimps and caps were removed from the aerobic replicates after gas collection.

#### 2.4. Chemical analysis

Gas samples were analyzed on an SRI Greenhouse Gas Monitoring Gas Chromatograph for  $CO_2$ ,  $CH_4$ , and  $N_2O$ . Standards were run every six sample injections for optimal quality assurance. Gas production rates from each soil replicate were determined for the aerobic samples as the increase in concentration relative to the initial levels on each sampling day. For the anaerobic soils production rates were calculated for the period between measurement days. The results from the  $N_2O$  analysis were nearly always not significantly greater than the minimum detection limit of the gas chromatograph; therefore, all  $N_2O$  data were removed from further consideration in this study. Additionally, while  $CH_4$  production was detected from a few of the aerobic headspace collections overall production rates were no significantly different than zero.

Remaining soils from the field collection were air-dried and passed through a 2-mm sieve for subsequent chemical analysis. Organic matter content was determined through loss on ignition at 550 °C for 5 h. The composition of the organic matter was determined through a series of sequential washes with an Ankom 200 fibre analyzer and other chemical tests (Rowland and Roberts, 1994; Inglett et al., 2012). A neutral detergent was first applied to remove the soluble soil organic matter (SOM) fraction. This fraction includes proteins, pectin, simple sugars, and lipids and waxes. The protein content of SOM was subsequently separated from this fraction with a Costech 4010 solid phase elemental analyzer. An acid detergent was then used to separate hemicellulose from the remaining SOM. The remaining SOM includes cellulose and lignin. These were further separated through acid hydrolysis with 72%  $H_2SO_4$ . The separations yield SOM fractions in decreasing reactivity/increasing recalcitrance. Fractions were standardized to the amount of organic matter present in the soil samples are expressed as a percentage of SOM.

#### 2.5. Data analysis

Gaseous carbon production was estimated as the slope of the linear regression through time on the samples. Differences in aerobic  $CO_2$ , anaerobic  $CO_2$ , and anaerobic  $CH_4$  production between soil types and temperature were assessed through two-way ANOVA and post-hoc Tukey's-HSD estimation. Differences in SOM content and fractions, anaerobic to aerobic carbon production ratios, anaerobic  $CO_2$  to  $CH_4$  production ratios, and  $Q_{10}$  temperature coefficients between peatlands and soil types were assessed with one-way ANOVA and Tukey's-HSD post-hoc comparisons. Linear and non-linear regression analyses were performed between the production data and soil quality data. All statistical analyses were performed in SYSTAT 12. Data were checked for normality and homogeneity with Shapiro-Wilk's and Levene's tests, respectively.

### 3. Results

#### 3.1. Soil characterization

Surface soils from the poor fen contained more organic matter (91.2%) than the rich fen (75.4%;  $p < 0.001$ ). The composition of that SOM also differed between the sites. The collected soils from the poor fen site were higher in the pectin, sugars, and lipids ( $p < 0.001$ ) but lower in protein ( $p < 0.01$ ) than soils collected from the rich fen. There was greater cellulose and hemicellulose in organic matter from the soils of the rich fen ( $p < 0.001$ ), but there were no differences in lignin content between the collected samples of the rich and poor fen sites (23.2 and 27.0%, respectively). The lingo-cellulose index was consequently higher in the poor fen SOM than the rich fen soil samples ( $p < 0.001$ ).

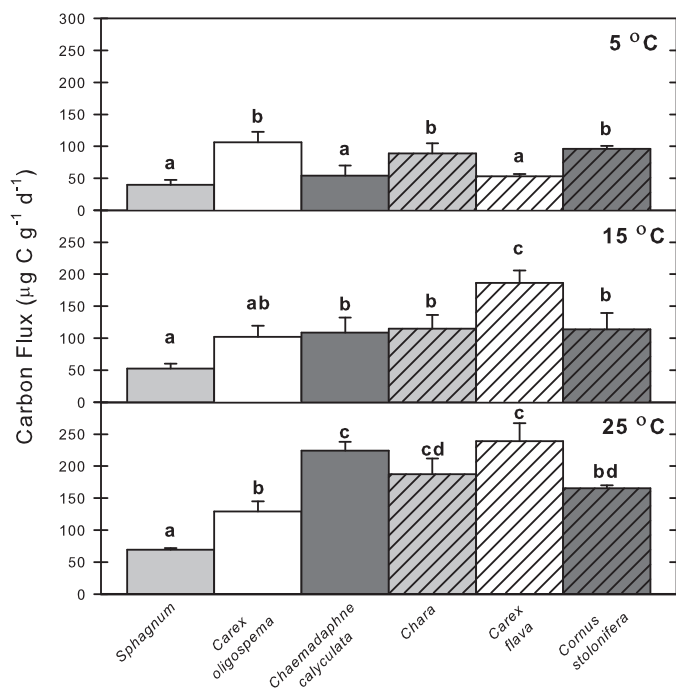
There were differences in SOM quantity and quality between soils derived from the same plant functional type in the two sites, and between the different plant functional types within each peatland. While there were no differences in SOM content in the poor fen soils, the rich fen soils ranged from a low of 54% under the filamentous algae community to a high of 82% in the sedge-dominated areas (Table 1). Lipids, pectin, and sugar content ranged from a low of 3% of SOM in the *Cornus* soils to a high of 41% in the *C. oligosperma* soils. Protein content in the SOM averaged ~11% except for greater amounts in soils found under *C. flava* and *Cornus* plants (16 and 20%, respectively). Hemicellulose and cellulose levels ranged from lows of 7 and 13%, respectively, in soils under the poor fen shrub *Chamaedaphne calyculata* to highs of 28 and 36%, respectively, in the rich fen filamentous algae *Chara* spp. soils. Correspondingly there was a five-fold increase in the proportion of SOM as lignin between soils under the *Chara* (8%) and *Chamaedaphne* (36%); the other four soil types had intermediary proportions of lignin. The differences between cellulose and lignin between the six different soil types led to a wide range in the lignin-to-cellulose ratio; soils under areas dominated by *Chamaedaphne* and *Sphagnum* communities had the highest ratio (0.64 and 0.50, respectively) and soils under the *Chara* the lowest (0.11).

**Table 2**

Results of two-way ANOVA of greenhouse-gas production affected by overlying soil type and incubation temperature.

Source	DF	F-scores		
		Aerobic	Anaerobic	
		CO <sub>2</sub>	CO <sub>2</sub>	CH <sub>4</sub>
Vegetation	5	39.258	51.249	131.297
Temperature	2	147.323	285.011	214.389
Veg * Temp	10	15.025	13.562	43.656

All values are significant at the  $p < 0.0001$  level.

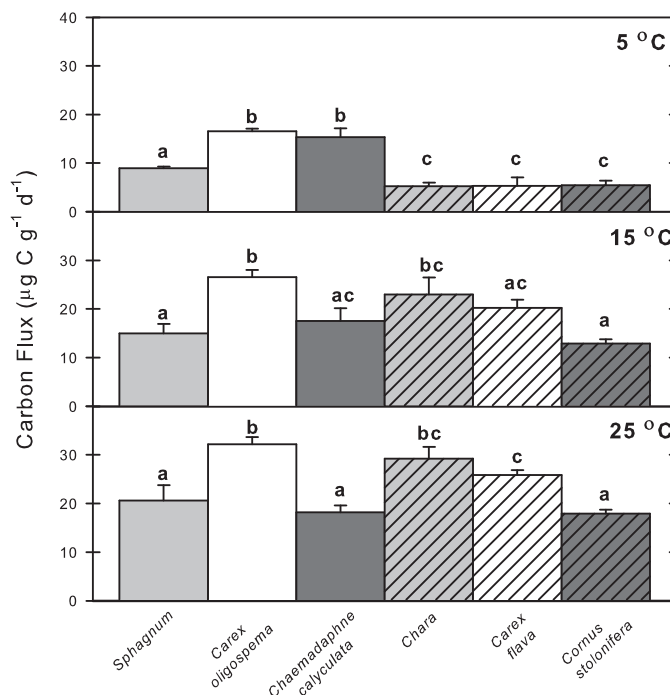


**Fig. 1.** Influence of peat type and incubation temperature on rates of aerobic CO<sub>2</sub> production. Letters represent significant differences ( $p < 0.05$ ) between peat types within an incubation temperature.

### 3.2. GHG-production potentials from soils at different sites and vegetation types

The soils under different vegetation types in the two peatlands produced different rates of carbon during the incubations; these differences were enhanced at higher temperatures. Overall, these differences were highly significant, with temperature having a higher control on production rates than the differences in composition of soils between the different areas of distinct vegetation (Table 2). In general, temperature had a very strong effect on anaerobic CO<sub>2</sub> production, while sampling area/vegetation and the interaction of vegetation area and incubation temperature had greater influences on CH<sub>4</sub> production.

Production of CO<sub>2</sub> from soil incubations under aerobic conditions of  $\sim 100 \text{ mg C g}^{-1} \text{ d}^{-1}$  at the cool temperature were twice as high in soils collected under *C. oligosperma*, *Chara*, and *Cornus* than the other three vegetation-collection areas (Fig. 1;  $p < 0.01$ ). At 15 °C aerobic CO<sub>2</sub> production increased in some species faster than others, which led to significantly higher potential rates under the *C. flava* soils ( $186 \text{ mg C g}^{-1} \text{ d}^{-1}$ ;  $p < 0.001$ ), with *Sphagnum*-derived peat producing the least ( $53 \text{ mg C g}^{-1} \text{ d}^{-1}$ ). This trend continued at the warmest incubation temperature, as soils obtained from *Sphagnum* communities had the lowest potential production rates of  $69 \text{ mg C g}^{-1} \text{ d}^{-1}$ , while *C. flava*-, *Chamaedaphne*- and *Chara*-derived peat soils had the highest rates (239, 224, and  $187 \text{ mg C g}^{-1} \text{ d}^{-1}$ , respectively).



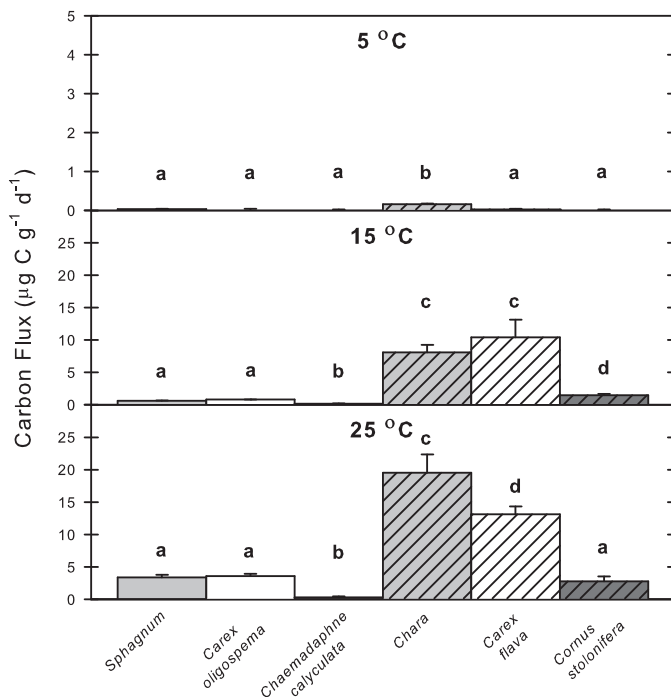
**Fig. 2.** Influence of peat type and incubation temperature on rates of anaerobic CO<sub>2</sub> production. Letters represent significant differences ( $p < 0.05$ ) between peat types within an incubation temperature.

Potential production rates of CO<sub>2</sub> in the anaerobic incubation in the 5 °C treatment were higher in the soils from the poor fen site than soils from the rich fen (Fig. 2). Soils from the poor fen site under vascular plant communities produced more carbon ( $\sim 16 \text{ mg C g}^{-1} \text{ d}^{-1}$ ) than soils from the *Sphagnum* areas ( $9 \text{ mg C g}^{-1} \text{ d}^{-1}$ ) at this incubation temperature ( $p < 0.05$ ). While there were significant differences in anaerobic CO<sub>2</sub> production rates at 15 °C ( $p < 0.05$ ) there were no apparent trends between soils from different vegetation types. Peat soils derived from the *Sphagnum* ( $21 \text{ mg C g}^{-1} \text{ d}^{-1}$ ), *Chamaedaphne*, and *Cornus* (each at  $18 \text{ mg C g}^{-1} \text{ d}^{-1}$ ) vegetation types had the lowest anaerobic CO<sub>2</sub> potential production rates at the warmest incubation temperature ( $p < 0.001$ ), whereas soils under the *C. oligosperma* had the highest ( $32 \text{ mg C g}^{-1} \text{ d}^{-1}$ ).

There was negligible CH<sub>4</sub> production from the anaerobic incubations at 5 °C, though the  $0.16 \text{ mg C g}^{-1} \text{ d}^{-1}$  from the *Chara*-derived peat was greater than the other five soil types ( $p < 0.01$ ; Fig. 3). Peat sampled from the rich fen produced significantly more CH<sub>4</sub> in the 15 °C incubations, with *Chara*- and *C. flava*-derived soils producing more (8 and  $10 \text{ mg C g}^{-1} \text{ d}^{-1}$ , respectively) than *Cornus* soils ( $1.5 \text{ mg C g}^{-1} \text{ d}^{-1}$ ). In the warmest incubation treatment potential methane production in soils from the area of the rich fen dominated by *Chara* more than doubled to  $20 \text{ mg C g}^{-1} \text{ d}^{-1}$ , which was significantly higher ( $p < 0.001$ ) than *C. flava* soils that increased to  $13 \text{ mg C g}^{-1} \text{ d}^{-1}$ . These CH<sub>4</sub> production potentials were much higher than soils from the *Sphagnum*, *C. oligosperma*, and *Cornus* areas ( $\sim 3 \text{ mg C g}^{-1} \text{ d}^{-1}$ ). Soils from the *Chamaedaphne* areas produced the least CH<sub>4</sub> ( $p < 0.001$ ) in the warmest incubation temperature at just  $0.19 \text{ mg C g}^{-1} \text{ d}^{-1}$ .

Overall, potential rates of anaerobic CO<sub>2</sub> production were 17% those of aerobic potential CO<sub>2</sub> production with a general, but non-significant, increase with increasing incubation temperature. Including the anaerobic potential CH<sub>4</sub> production rates into the anaerobic carbon component slightly increased the anaerobic to aerobic carbon production potential to 19%. The anaerobic to aerobic C production ratio was highest in *Chara*, *C. oligosperma*, and *Sphagnum* soils ( $\sim 28\%$ ). This ratio ranged between 8 and 16% in



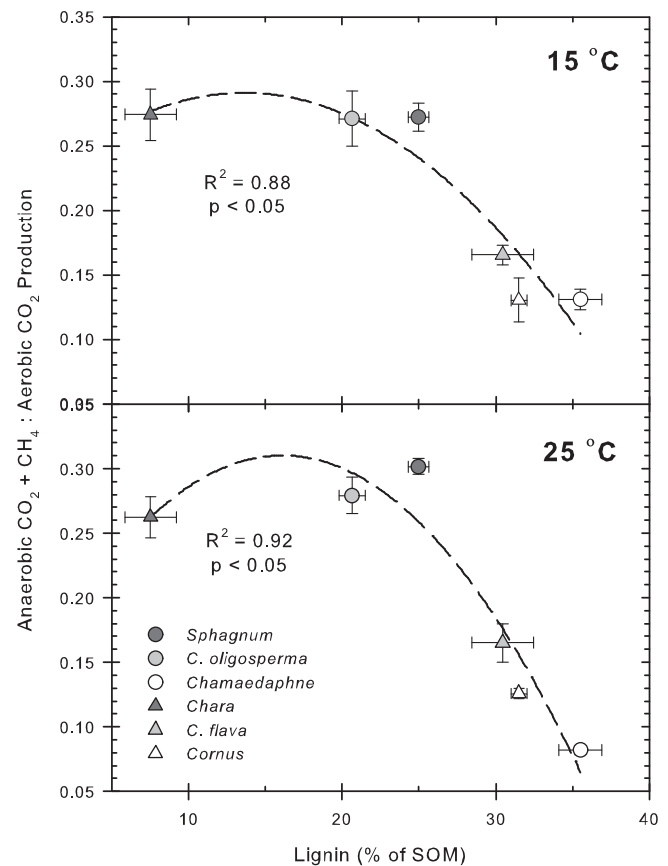


**Fig. 3.** Influence of peat type and incubation temperature on rates of anaerobic CH<sub>4</sub> production. Letters represent significant differences ( $p < 0.05$ ) between peat types within an incubation temperature.

the other three soil types at 15 and 25 °C. There were significant quadratic correlations ( $p < 0.05$ ) between the ratios of anaerobic to aerobic potential production and the proportion of lignin in the peat SOM at the two higher incubation temperatures (Fig. 4). There was minimal change in anaerobic to aerobic C production in soils with lignin contents up to 25% of SOM; increased lignin proportions beyond this level led to steep declines in the anaerobic to aerobic ratio (Fig. 4).

The ratio of potential anaerobic CO<sub>2</sub> production to CH<sub>4</sub> production differed between soil types ( $p < 0.001$ ) at all incubation temperatures, generally following the order *Chamaedaphne*-derived soils having the highest ratios, followed by *C. oligosperma*-, then *Cornus*- and *Sphagnum*-, then *C. flava*-, with *Chara*-derived soils the lowest (Fig. 5). Due to very low methane production rates in the 5 °C incubation the anaerobic CO<sub>2</sub>:CH<sub>4</sub> was very high in soils, particularly under *Chamaedaphne* and *C. oligosperma* communities, where ratios were 741:1 and 512:1, respectively. Soils from the *Chara* areas had the lowest anaerobic CO<sub>2</sub>:CH<sub>4</sub> ratios at all three incubation temperatures (32:1, 3:1, and 1.5:1 in the 5, 15, and 25 °C incubations, respectively) due to the elevated CH<sub>4</sub> production from these soil samples. There were significant exponential correlations between the soil LCI and the ratio of anaerobic CO<sub>2</sub> to CH<sub>4</sub> potential production rates at all three incubation temperatures (Fig. 5). The significance of these correlations increased with increasing temperature ( $p < 0.05$ , 0.01, and 0.0001 at 5, 15, and 25 °C, respectively), as did the slope of the exponential correlation.

Overall, increasing temperature led to increased potential rates of aerobic CO<sub>2</sub> and anaerobic CO<sub>2</sub> and CH<sub>4</sub> production for the temperate peatland soils tested, and the Q<sub>10</sub> values differed between soil types ( $p < 0.001$ ; Table 3). There was also considerable variation between aerobic and anaerobic Q<sub>10</sub> responses. Potential aerobic CO<sub>2</sub> production was minimally impacted by increased temperatures in *C. oligosperma* soils (Q<sub>10</sub>=1.10), but aerobic CO<sub>2</sub> Q<sub>10</sub> values were significantly greater in *Chamaedaphne* and *C. flava* soils (2.06 and 2.12, respectively). The high Q<sub>10</sub> for *C. flava* soils con-



**Fig. 4.** Effect of SOM lignin proportion on the ratio of anaerobic CO<sub>2</sub> plus CH<sub>4</sub> production to aerobic CO<sub>2</sub> production at the warmer two temperatures. Whiskers of each soil type represent standard errors of lignin and greenhouse-gas production ratio. Dashed line is the modelled quadratic fit of the data with R<sup>2</sup> and significance as indicated. There was no significant correlation between lignin and the anaerobic to aerobic production ratio at the 5 °C incubation.

**Table 3**

Mean Q<sub>10</sub> (5–25 °C) values for greenhouse-gas production from poor and rich fen near-surface soils.

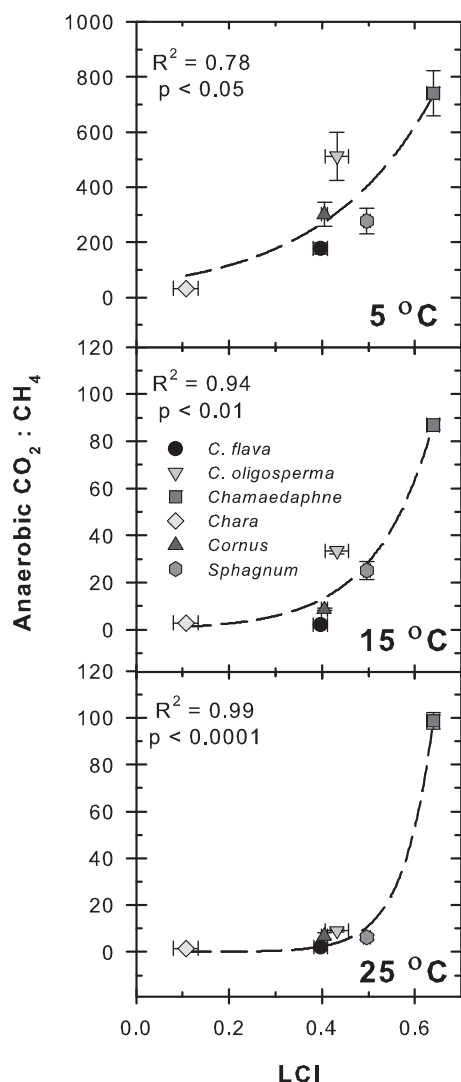
Soils under a community dominated by:	CO <sub>2</sub> Production		Methanogenesis
	Aerobic	Anaerobic	
<i>Carex oligosperma</i>	1.10 <sup>a</sup>	1.39 <sup>ab</sup>	10.39 <sup>a</sup>
<i>Chamaedaphne calyculata</i>	2.06 <sup>b</sup>	1.09 <sup>b</sup>	2.98 <sup>b</sup>
<i>Sphagnum capillifolium</i>	1.33 <sup>a</sup>	1.51 <sup>ab</sup>	10.10 <sup>a</sup>
<i>Carex flava</i>	2.12 <sup>b</sup>	2.27 <sup>c</sup>	21.40 <sup>c</sup>
<i>Chara</i> spp.	1.46 <sup>a</sup>	2.38 <sup>c</sup>	16.01 <sup>a</sup>
<i>Cornus sericea</i>	1.31 <sup>a</sup>	1.82 <sup>ac</sup>	12.30 <sup>a</sup>
F-scores	26.439	19.485	25.589

F-scores represent results of one-way ANOVA.

Superscript letters denote significant differences ( $p < 0.05$ ) between the soil types for the corresponding production pathway.

tinued for anaerobic C production (both CO<sub>2</sub> and CH<sub>4</sub>); however, *Chamaedaphne* soil Q<sub>10</sub> values were significantly lower than the other soil types for both anaerobic CO<sub>2</sub> (1.09) and methanogenesis (2.98). Methanogenic Q<sub>10</sub> values in the other soil types were high, ranging from 10.10 for *Sphagnum* soils to 21.4 in *C. flava* soils.

The differences in the SOM quality had a significant control on the observed differences in Q<sub>10</sub> between species (Fig. 6). Aerobic CO<sub>2</sub> production in response to increasing temperature was related to the lignin to cellulose index ( $p < 0.05$ ); generally increasing amounts of lignin relative to cellulose led to greater Q<sub>10</sub> values. Both anaerobic CO<sub>2</sub> and CH<sub>4</sub> Q<sub>10</sub> values increased linearly with

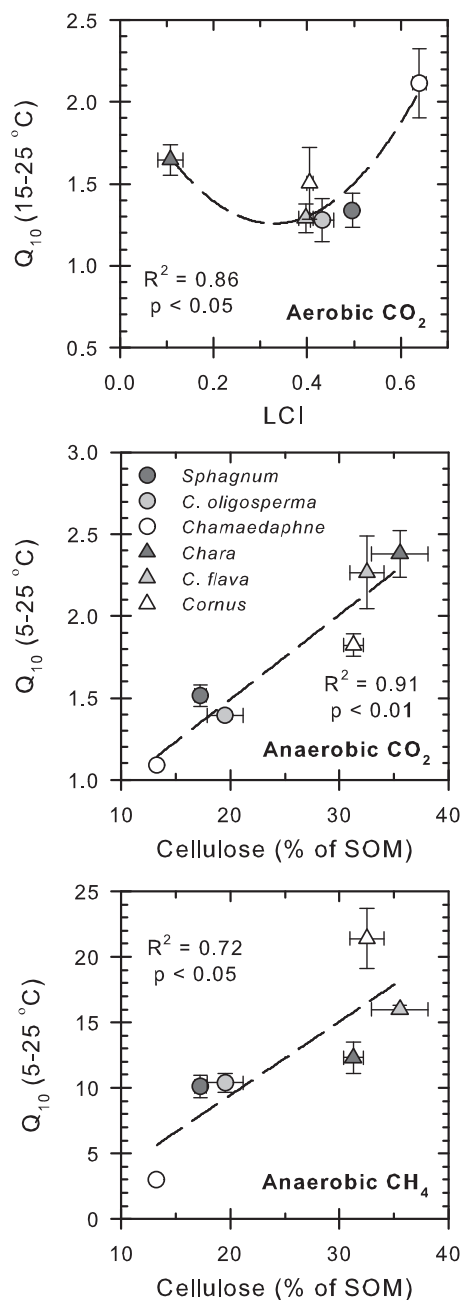


**Fig. 5.** Relationship between the lignin-to-cellulose index and the ratio of anaerobic  $\text{CO}_2$  to  $\text{CH}_4$  production at the three incubation temperatures. Whiskers of each soil type represent standard errors of LCI and greenhouse-gas production ratio. Dashed line is the modelled second-order exponential fit of the data with  $R^2$  and significance as indicated.

increasing proportions of cellulose in the SOM pool. This relationship was stronger for anaerobic  $\text{CO}_2$  production ( $R^2 = 0.91$ ;  $p < 0.01$ ) than for  $\text{CH}_4$  ( $R^2 = 0.72$ ;  $p < 0.05$ ). In general, the anaerobic  $Q_{10}$  values were lower from the sampled poor fen soils than from the rich fen soils.

#### 4. Discussion

This study demonstrated that potential rates of  $\text{CO}_2$  and  $\text{CH}_4$  production from near-surface peatland soils differ in accordance with differences in overlying vegetation type. These differences propagate with increasing temperature between both vegetation type and aerobic and anaerobic conditions. The rates of greenhouse-gas production observed in the sample incubations were controlled by the carbon quality of that incubated peat soil. Overall, *Carex flava*-soils had the highest potential rates of carbon production, particularly under aerobic conditions; however, high levels of  $\text{CO}_2$  production were also found in incubated *C. oligosperma*-soils under waterlogged, anaerobic conditions, while *Chara* spp.-soils had the highest rates of  $\text{CH}_4$  production.



**Fig. 6.** Calculated  $Q_{10}$  values presented by the SOM component that best described the data for each incubation temperature. Whiskers of each soil type represent standard errors of SOM component and  $Q_{10}$ . Dashed line is the modelled quadratic (aerobic  $\text{CO}_2$ ) and linear (anaerobic  $\text{CO}_2$  and  $\text{CH}_4$ ) fit of the data with  $R^2$  and significance as indicated.

##### 4.1. Influence of SOM quality of gaseous carbon production dynamics

There were very clear differences in SOM quality between the soils collected from the poor and the rich fens. It is possible these differences reflect fundamental differences between poor and rich fens in general. The two sites were underlain by similar geologic material and were in similar hydrogeomorphic settings, suggesting the observed SOM differences may reflect subtle differences in the chemical makeup and subsequent breakdown of the similar vegetation between the two fens. On the other hand, it is also possible the differences in SOM quality arise because of site-specific condi-

tions not accounted for in the experimental design. More research is needed on the underlying cause of variability in peatland SOM quality, especially given the control this quality has on mineralization and greenhouse-gas production in response to temperature increases.

Within each site differences in overlying vegetation cover was correlated with differences in the various fractions of soil carbon in the near-surface peat (Table 1). The soil samples were collected from areas within 100 m at the poor fen and 150 m at the rich fen, suggesting small scale changes in vegetation can have strong effects on the residual carbon deposited in the peat profile. In both sites the soils dominated by overlying shrubs (*Chamaedaphne* and *Cornus*) contained higher proportions of lignin; rich fen sedges (*C. flava*) also appeared to result in elevated lignin in the underlying soils relative to poor fen sedges (*C. oligosperma*). The peat deposited in areas dominated by the filamentous algal species *Chara* had considerably less lignin, with proportional increases in cellulose and hemicellulose. The proportion of SOM as lignin, and in particular the lignin to lignin plus cellulose index has been shown to exert a key control on decomposition (Melillo et al., 1989; Moore et al., 2007; Inglett et al., 2012; Sihi et al., 2016; Inglett et al., 2012; Sihi et al., 2016), with increasing LCI resulting in lower rates of decomposition and carbon production. Results of the present study broadly agree with this, but there were differences to the trend.

There were similar LCI values between the two sedge and *Cornus* soils, yet variable differences in aerobic and anaerobic potential rates of carbon production between the three soil types. Observed aerobic CO<sub>2</sub> production rates followed the trend *Cornus* > *C. flava* > *C. oligosperma*; anaerobic CO<sub>2</sub> production rates followed the opposite order, while *C. flava* had higher CH<sub>4</sub> potential production rates than the other two soil types with equivalent LCI. *Chamaedaphne* and *Sphagnum* soils had the highest LCI, with *Sphagnum*-derived peat having significantly lower proportions than the shrub soils (Table 1); however, rates of aerobic CO<sub>2</sub> production were also significantly lower in the lower-LCI *Sphagnum* soils (Fig. 1). There were similar anaerobic CO<sub>2</sub> rates between these two soil types (Fig. 2) and *Chamaedaphne* soils did produce significantly more CH<sub>4</sub> than the *Sphagnum* soils (Fig. 3). Additionally, peat derived from *Chara* soils contained very little lignin and consequently low LCI, and had the highest observed rates of CH<sub>4</sub> production.

These findings suggest that the LCI has a stronger control on anaerobic than aerobic production, which is supported by Figs. 4 and 5. Peat lignin contents less than 25% appeared to have no influence on the ratio of potential anaerobic to aerobic production; however, greater proportions led to very steep declines in this ratio (Fig. 5)—indicating proportionally lower rates of anaerobic decomposition. Furthermore, there were significant exponential increases in anaerobic CO<sub>2</sub> to CH<sub>4</sub> production potential with increasing LCI (Fig. 5), as proportionally less gaseous carbon production was due to methanogenesis with increasing LCI. Therefore, results of this study suggest increasing lignin content in peat (and hence increasing LCI) may progressively lead to greater ratios of aerobic decomposition under lower water table/soil moisture conditions relative to times of high water tables, and higher fermentation relative to methanogenesis while saturated. Shaver et al. (2006) observed proportionally lower decomposition in sedge peat (high in lignin) relative to tussock and heath soils (lower lignin) in wet conditions compared to dry conditions. Lower rates of labile carbon (i.e., higher lignin) have been shown to limit methanogenesis (Yavitt and Lang, 1990). Rates of methanogenesis increase in peat soils high in low-molecular weight organic acids and simple sugars (Ström et al., 2012; Sjögersten et al., 2016). High proportions of recalcitrant lignin may strongly limit the breakdown of SOM into these suitable substrates.

#### 4.2. Temperature sensitivity of carbon gas fluxes from peat soils

The results of this study add to the body of literature demonstrating the increased rates – oftentimes nonlinearly—of greenhouse-gas production from surface peat soils due to rising temperatures (Treat et al., 2014; Diakova et al., 2016; Sihi et al., 2016; Wilson et al., 2016). In the present study temperature had a stronger effect on rates of aerobic CO<sub>2</sub> and anaerobic CO<sub>2</sub> and CH<sub>4</sub> production than did the effect of overlying vegetation through its influence on SOM (Table 2). Q<sub>10</sub> values for aerobic and anaerobic CO<sub>2</sub> production varied by 2.5 times between the different soil types and are on the low end of the range reported in previous studies (~1–16; Moore and Dalva 1993; McKenzie et al., 1998; Inglett et al., 2012; Zhu et al., 2015; Sihi et al., 2016). The higher values from the literature were found in more northern peatlands where soils were subjected to temperatures not normally found in nature. The highest incubation temperature in the present study was only slightly (~5 °C) higher than peak summer soil temperatures at the two peatlands (Duval, 2010; Radu, 2017). There were no clear trends in Q<sub>10</sub> variability between peat collected from the rich and poor fens, or by soils sampled under different vegetation types (shrubs vs. sedges vs. non-vascular plants).

In general, potential anaerobic production was slightly more responsive to increased temperatures than potential aerobic CO<sub>2</sub> production, with greater Q<sub>10</sub> values under anaerobic conditions for five of the six soil types tested (Table 3). Despite this comparative increase, the ratio of anaerobic to aerobic production did not increase with increasing temperature for each soil type (as seen in Fig. 4). On the other hand, Q<sub>10</sub> values for methane production increased two to eight times from anaerobic CO<sub>2</sub> production, in part because of the very low potential production rates in the coldest incubation temperature (Fig. 3). The increased sensitivity to temperature for methane production is well established (Segers, 1998).

The increased observed CH<sub>4</sub> production at higher temperatures led to an overall decrease in the anaerobic CO<sub>2</sub> to CH<sub>4</sub> potential production ratio (Fig. 5). Due to very low CH<sub>4</sub> production in the 5 °C incubation these ratios were very high at that temperature (740:1 from the *Chamaedaphne* soils). The decrease in this ratio with increasing temperature varied between the soil types. Anaerobic CO<sub>2</sub> to CH<sub>4</sub> potential production ratios for the sedge soils (*Carex flava* and *C. oligosperma*) decreased 98% between the coolest and warmest incubation temperatures, with nearly all the decrease occurring between 5 and 15 °C. Between 15 and 25 °C this ratio decreased marginally for *C. flava* soils, but 75% for *C. oligosperma* soils. Anaerobic CO<sub>2</sub> to CH<sub>4</sub> ratios decreased by 50% in *Chara* soils between 15 and 25 °C, but the ratio stayed the same for *Chamaedaphne* soils. At 20 and 30 °C Inglett et al. (2012) found the anaerobic CO<sub>2</sub> to CH<sub>4</sub> potential production ratio ranged from ~1 to 4 for five subtropical peatland soils covered by contrasting vegetation. In the present study this ratio ranged between 1.5 for *Chara*- and 9 for *C. oligosperma*-soils at 25 °C (ratio of 99:1 in *Chamaedaphne* soils). These differences in rates of CH<sub>4</sub> production and the proportions between anaerobic carbon production pathways suggest soil organic matter quality has a strong control on the sensitivity of peat decomposition to temperature.

#### 4.3. Control of SOM on temperature sensitivity

The proportions of cellulose and lignin in the SOM had strong controls on the temperature sensitivity of the peat incubations to greenhouse-gas production. For all three temperature incubations there was an exponential relationship between the lignin to cellulose index (LCI) of the peat and the resultant ratio of anaerobic CO<sub>2</sub> production to CH<sub>4</sub> production (Fig. 5). As both the strength of the relationship and the steepness of the exponential response

increased with temperature there would appear to be a synergistic effect between SOM quality and temperature. Lower LCI values indicate lower amounts of lignin relative to cellulose; methanogenesis requires simple, low-molecular weight carbon compounds and is inhibited by the complex, recalcitrant carbon found in lignin (Yavitt and Lang, 1990; Sjögersten et al., 2016). Increased soil temperature in peatlands has been shown to produce non-linear increases in rate of fermentation (Updegraff et al., 1998; Waddington et al., 2001; Szafraniek-Nakoneczna and Stepniewska, 2014). Therefore, it is likely that microbial breakdown of cellulose to simple sugars is stimulated at higher temperatures, producing organic carbon products that serve as substrate for methanogenesis.

There were clear differences in the proportion of cellulose and lignin between the soils collected from the two sites in this study, which also produced differences in LCI between the rich and poor fen soil types (Table 1). These differences explained the observed variability in the  $Q_{10}$  values for all forms of greenhouse-gas production (Fig. 6). The quadratic relationship between LCI and the  $Q_{10}$  response to temperature of aerobic  $CO_2$  represents a decreasing relationship in the poor fen soils, and an increasing relationship in the rich fen soils. The increased  $Q_{10}$  values in response to declining SOM quality (higher lignin content) in the rich fen soils is not supported by findings from subtropical and permafrost peatlands (Inglett et al., 2012 and Sjögersten et al., 2016, respectively). On the other hand, Hiltunen et al. (2013) found increased  $Q_{10}$  values with increasing recalcitrant carbon in boreal peat. It is possible that increased temperatures stimulates microbial breakdown of the complex lignin molecules (Leifeld and Fuhrer, 2005). Due to the relative ease of microbial breakdown of simpler molecules under anaerobic conditions the proportion of cellulose in SOM explained the trends in both anaerobic  $CO_2$  and  $CH_4$   $Q_{10}$  responses (Fig. 6). This is in general agreement with previous findings (Inglett et al., 2012; Sihi et al., 2016).

#### 4.4. Moving from bench-top incubation results to field-scale generalizations

This study used replicates of 10 g of peat collected from contrasting areas of two study sites; the 10 g were subsamples of homogenized peat. Thus, by definition, this experiment represents a necessary abstraction from *in situ* conditions in order to isolate the effects of temperature, SOM quality, and their interaction. In sample collection and homogenization the peat bulk density and porosity are destroyed, and the effects of live-plant matter, such as enhanced gas transport through vascular tissue and micro-site differences in soil temperature, moisture, and aeration, are removed. Vascular plants serve as conduits for gas exchange between the atmosphere and the soil subsurface, whereas *Sphagnum* moss and *Chara* algae do not (Mitsch and Gosselink, 2015). Furthermore, *Carex* species are capable of vast aerenchyma formation to increase  $O_2$  diffusion to anaerobic root zones, which also enables increased  $CH_4$  flux to the atmosphere (Strom et al., 2005); shrub species such as *Cornus stolonifera* and *Chaemadaphne calyculata* lack this adaptation (Shannon and White, 1994). While most of the decomposition and  $CH_4$  production that does occur in the soil profile occurs in the upper 20-cm there is some production at depth (Moore and Dalva, 1993; Wilson et al., 2016); this study did not look at depth-integrated rates of production. While bulk density of peat can vary by over an order of magnitude (Yu, 2012; Lawson et al., 2015), increasing bulk density can lead to lowered  $CH_4$  production (Laing et al., 2010) and flux (Nwaishi et al., 2016). As such, the results presented here represent potential production rates from extracted soil samples and cannot directly be transferred to field-scale differences.

Nevertheless, generalizations can be made as to how the SOM-quality dependence of temperature sensitivity on peat  $CO_2$  and  $CH_4$  production in lab slurries will impact fluxes of greenhouse gases from peatlands. Growing season fluxes of  $CO_2$  to the atmosphere averaged 1.8, 1.3, and 4.8  $g\ m^{-2}\ d^{-1}$  from the poor fen moss, sedge, and shrub communities, respectively, of this study (Radu, 2017). Rates of  $CH_4$  emission to the atmosphere for the moss, sedge, and shrub poor fen communities averaged 17.7, 15.1, and 6.2  $mg\ m^{-2}\ d^{-1}$ , respectively (Radu and Duval, submitted). These field flux data are in line with the results of this study, where *Chaemadaphne*-derived soils had higher aerobic  $CO_2$  production (Fig. 1) but lower anaerobic  $CH_4$  production (Fig. 3) than *Sphagnum*-derived soils. Therefore, these findings support the conclusion that in addition to *in situ* conditions created by the overlying vegetation, the SOM quality derived from the vegetation has an effect on greenhouse-gas fluxes to the atmosphere from the different vegetation communities.

There are few direct attempts in the literature to link micro-scale determination of the interaction of controlling processes with the observed field-scale gas fluxes, at least in relation to soil carbon quality. Recently, Hodgkins et al. (2015) made the link between lab incubations and pore-water  $CH_4$  and  $CO_2$  concentrations measured in the field, but did not relate the pore-water values to field efflux. Sjögersten et al. (2016) determined the role of SOM quality on greenhouse-gas production through field and lab measurements, but did not measure fluxes to the atmosphere. Earlier work by Moore and Dalva (1993) measured both greenhouse-gas production values from incubations and fluxes from intact soil cores. From their experiments they were able to directly relate  $CH_4$  production differences between wetland types to observed fluxes from the cores. Shannon and White (1996) found higher pore-water concentrations of acetate and  $CH_4$  under areas dominated by grasses and sedges compared to *Chaemadaphne* areas. They were able to relate these differences to higher  $CH_4$  flux from the sedge area relative to the shrub area in their earlier field study (Shannon and White, 1994). Further research is required to directly link the relationships between subsurface processes and greenhouse-gas production to observed plot- and field-scale greenhouse-gas fluxes from peatlands to the atmosphere in order to test and refine mechanistic models of peatland carbon gas dynamics in the face of climate and land-use change.

## 5. Conclusions

The results of this study support peatland management efforts aimed to reduce carbon efflux, maintain peatland carbon neutrality, and increasing carbon storage (Cui et al., 2015). This study adds to the growing body of literature recognizing that the varied vegetation communities of peatlands have a strong control on peatland carbon balance through species-specific controls on primary production, ecosystem respiration, and  $CH_4$  flux (Ström et al., 2005; Mahmood and Strack, 2011; Carter et al., 2012; Leifeld et al., 2012; Juszczak et al., 2013; Turetsky et al., 2014). Increasing global air temperatures will increase near-surface soil temperatures, which will have varying effects on aerobic  $CO_2$ , anaerobic  $CO_2$ , and  $CH_4$  production from soils differing in SOM quality (Moore and Dalva, 1993; Inglett et al., 2012; Sihi et al., 2016; Wilson et al., 2016); this quality is in large part controlled by overlying vegetation (Heller et al., 2015; Pinsonneault et al., 2016). Therefore, knowledge of the relationship between peat type (SOM quality) and rates of greenhouse-gas production and their sensitivity to temperature is crucial to the understanding and prediction of future carbon emissions from temperate peatlands particularly as the spatial patterning of surface vegetation changes in response to climate change.



At current soil temperatures ( $\sim 15^{\circ}\text{C}$ ) there was a great range (2:1 to 87:1) in the ratio of anaerobic  $\text{CO}_2$  to  $\text{CH}_4$  production from the soils (Fig. 5). An increase in soil temperature to  $25^{\circ}\text{C}$  shrunk this range between soil types, with most soils producing between 1.5 and 9 times more  $\text{CO}_2$  than  $\text{CH}_4$  when anaerobic (*Chamaedaphne* soil ratio was still near 100:1). Increasing soil temperatures at these two fens will likely lead to greater rates of  $\text{CH}_4$  emission. This is especially problematic given the much greater global warming potential (GWP) of  $\text{CH}_4$  relative to  $\text{CO}_2$ . On the other hand, anaerobic C loss was between 7 and 30% of aerobic C loss in this study (Fig. 4), with nearly an order of magnitude more anaerobic  $\text{CO}_2$  than  $\text{CH}_4$  production. Thus, despite the higher  $\text{CH}_4$  production rates at higher temperatures this study conclusively demonstrates that maintenance of a high water table to promote anoxia will significantly minimize greenhouse-gas loss and lead to overall lower GWP from these peatlands.

Vegetation community shifts in peatlands will alter the magnitude of the greenhouse-gas loss to the atmosphere. Regardless of temperature the peat derived from *Chamaedaphne* shrubs contained significantly more lignin and consequently had higher LCI (Table 1). This high LCI resulted in significantly less  $\text{CH}_4$  production than the other soil types (Fig. 3), with equivalent rates of anaerobic  $\text{CO}_2$  production (Fig. 2). Conversely, water table lowering leading to aerobic conditions in surface peats will lead to elevated rates of aerobic  $\text{CO}_2$  production from these shrub soils (Fig. 1). Shrub expansion is a likely consequence in northern and temperate peatlands (Ward et al., 2013; Munir et al., 2015; Walker et al., 2015), and greater understanding of their impacts on near-surface peat soil carbon quality and mineralization is warranted. Overall, *Sphagnum*-derived soils produced the least amount of carbon, with significantly lower aerobic  $\text{CO}_2$  fluxes at all temperatures and low rates of anaerobic carbon production. Long-term maintenance and/or proportional expansion of *Sphagnum* vegetation would appear to be central to minimizing carbon loss from temperate peatlands; however, the increased degradation of inhibitory phenolics in peat soil with increased temperature may change these patterns (Pinsonneault et al., 2016). Additionally, the role of shrub vegetation and its influence on lignin stocks in the peat minimizing  $\text{CH}_4$  production is worthy of future study.

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